STUDIES FOR STUDENTS

THE DEVELOPMENT AND GEOLOGICAL RELATIONS OF THE VERTEBRATES.

The object of these studies is in no wise to attempt to furnish a course in vertebrate palæontology, but rather to place before the student of geology, who has no time for the study of the morphological and phylogenetic questions involved, a brief statement of the results achieved by the workers in the more narrow field. The value of vertebrate remains as indicators of the time changes in the past is so well recognized that it is hoped that an orderly summary of the fossil vertebrates, with a brief indication of the lines along which they have developed, and references to the most helpful literature, may be of value to the student, both within the limits of these articles and in aiding him to extend the work by collateral reading.

PART I. THE FISHES.

FISHES are, in the popular language of Bashford Dean, "back-boned animals, gill-breathing, cold-blooded, and provided with fins." This definition may well be used if we remember that the "back-bone" is not always bony, that it may be entirely cartilaginous or only partly ossified. A similar condition may be found in all the other bones of the body and is the chief reason that the early history of the fishes is hidden in the deepest obscurity, for it is one of the most commonly recognized facts of palæontology, as well as one of the most deplorable, that only under the most favorable conditions can the soft structures of any body be preserved. From this it is easily understood why the earliest remains of fishes that we possess are those of forms in which the skeleton has progressed so far as to be formed of solid cartilage at least, and generally of cartilage with local ossification or calcification.

The following classification of the larger groups of the fishes is in general use :

Class : PISCES.
- Sub-Class : *Marsupiobranchii.*
- *Ostracodermi.*
- *Elasmobranchii.*
  - Order : *Selachii.*
  - *Batoidi.*
- Sub-Class : *Holocephali.*
- *Dipnoi.*
  - *Sirenoidei.*
  - *Arthrodira.*
- Sub-Class : *Teleostomi.*
  - Order : *Crossopterygii.*
  - *Actinopterygii.*
    - Sub-Order : *Chondrostei.*
    - *Teleocephali.*

The first of these, the *Marsupiobranchii*, are not well understood in their relations to the true fishes. The most common of the group are the hagfishes and the lampreys of the present time. They differ from all other vertebrates by the entire absence of the lower jaw and of the pelvic and pectoral girdles of bone that support the hind and the fore limbs. Whether these conditions are the primitive stages of a developing fish or are the final stages of a degenerate structure, is still an unsettled question, and it is at this point of difficulty that we turn to the palæontological record. However, we can gain but little from the palæontology of the forms. A single specimen from the Old Red Sandstone of Scotland is the representative of the fossil *Marsupiobranchii*, and it is even doubtful whether this specimen is correctly referred to that group. The specimen shows the presence of well defined rings in the position of the vertebræ, a stage in advance of the recent forms, which would indicate for them a degenerate structure.

The earliest remains of fishes known are from the Lower Ordivician rocks of the Grand Canyon region of the United States. These are the very imperfectly preserved remains of what seem to be scales and bones of fishes whose affinities cannot be made out from the material.

Before attempting to take up the different forms of the true fishes it may be well to consider briefly those points in the anatomy of fishes in general where changes have taken place resulting in the modern type of the bony fishes. There are three regions in the skeleton that have been used more than any others in making out the different groups of the fishes and their phylogenetic development: 1. The gradual ossification of all the bones of the body. 2. The development of the vertebræ. 3. The development of the fin of the modern type.

The first of these is the gradual process of strengthening the skeleton by the addition of solid matter which has been at work ever since the origin of the class and is still incomplete in many forms. It is only in the last sub-order of the *Teleostomi*, the *Teleocephali*, that the process is at all complete. Before the actual formation of bone in the supporting tissues of the body the cartilage was frequently strengthened by the deposition of calcareous particles. This is the condition found in the remains of most of the early sharks.

The second process, the development of the vertebræ, is of considerable importance not only in the development of the fishes, but as we shall see, in the earliest of the *Amphibia* as well. The most primitive condition of the spinal column is such as is well illustrated in the *Amphioxus*, one of the simplest of all the vertebrate phylum, the column in this case consisting of a continuous rod of cartilage, the notochord, extending through the body from the anterior to the posterior end and lying near to the dorsal side of the body. It is protected by several layers or sheaths of membrane in which the future vertebræ are developed. The development of the bony covering of this rod is foreshadowed by the appearance of the cartilaginous rings that have the same serial arrangement as the vertebræ of the more advanced types. A very important thing about the development of the vertebræ is the development on the superior and the inferior faces of the chordal sheath of bony arches that appear before the body proper, or centrum, of the vertebræ. The superior of these, the neural arch, protects the spinal cord

throughout the length of the vertebral column. The second is developed to the fullest extent only in the caudal portion of the column and there furnishes a protection for blood vessels. These arches may or may not be attached to the centrum in the adult form, but the bases are the first points of ossification and the rest of the vertebræ develops between them. The process is not complete in all of the fishes, and the gradual completion of the vertebræ is of great aid in determining the position of some of the fossil forms (Fig. 1).

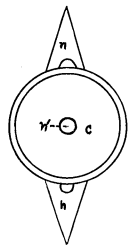

Fig. 1. Schematic view of a vertebra. *n*, neural arch; *c*, centrum; *h* hæmal arch; *w*, notochordal canal.

The third, and perhaps the most important of the three regions of development is the formation of the fins, both paired and median. Whatever may have been the original form of the fish the first thing in the evolution demanded by their peculiar environment must have been the development of some form of keel that would not only aid the fish in its progress through the water, but would enable it to maintain any desired position both as to the relative depth below the surface of the water and as to lateral displacement. The first step in the accomplishment of this end was the development of long fins extending from the head to the tail. One pair of these was developed on the median dorsal and ventral lines, and persists in the dorsal, caudal, and ventral fins of the existing fishes. The second pair extended along each side of the body in a plane at right angles to the first and divided the body into approximately equal parts above and below. The paired fins, the pectoral and the ventral, are supposed to be remnants of these lateral folds or fins.

The development of the fins seems to have followed a very definite line that has served as a great aid in making out the classification of the various fossil and recent forms. Undoubtedly the first stage of the development of the fins was the formation of the long folds of the skin that were without any internal support, and capable of very complex, wavelike motion, and without any great power of resistance to impressed forces. Of this stage we do not have any trace in the preserved fossil forms for the reason already assigned, that soft parts are not preserved except under the most exceptional circumstances. We should expect it to occur in the remains of the *Marsupiobranchii*, if at all, but the single specimen preserved, *Paleospondylus*, does not show any evidence of such a fold. The function of the fin fold, to preserve the equilibrium of the fish, would demand some degree of resistance in the fold, and the next stage of the fin must have been the appearance of fine, hair-like rays of horny material, confined to the dermal part of the fold and not joined to the body proper. These were many in number, and only served to stiffen the fin without strengthening its attachment to the body. These fine rays have been called the actinotrichia. The second stage in the development of the fins was the fusion of certain of these actinotrichia at points of the greatest strain in the fins into larger and more solid elements that afforded a much greater power of resistance at those points. The comparatively large and strong cartilaginous rods thus formed have received the name of radials. The same necessity of resisting outside forces that caused the union of the actinotrichia to form the radials demanded a stronger attachment of the radials to the body wall of the fish, and this was accomplished by the separation of the proximal portion of the radial as a separate element, which became elongate and penetrated into the body wall, affording a very strong support to the radials. This proximal section is called the basal (Fig. 2).

Up to this point in the development of the fins the history of the paired and the unpaired fins is regarded as practically the same, for the paired fins were as yet but undifferentiated parts

of the lateral body folds. The reason for the development of one portion of the lateral fins over another is not well understood, but it has been suggested that at points of especial strain in the fold, points where, from the mechanical advantage of their

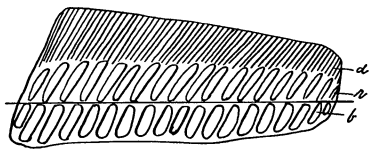

FIG. 2. Schematic unpaired fin; *b*, basal, *r*, radial; *d*, dermal margin of fin (after Smith-Woodward).

position, certain parts of the fold were able to assist in the propulsion of the body through the water, that the fins were especially well developed, and that there appeared lappetlike prominences in the position of the present paired fins. As these lappets assumed more and more of the function of swimming organs, and less of balancers, they required an even stronger support than before, and this was accomplished by the fusion of the basals together and also of the radials, though to a less extent. As the lappets of the lateral fin grew in importance, the intermediate portion dwindled away until all trace of the original fold is lost between and beyond the paired fins. The final step in the development of the fins was the appearance beyond the distal ends of the radials of fine dermal elements that have much the appearance of the original actinotrichia. These serve the purpose of supporting the web at the extremity of the fins.

Another line of development of the fishes is closely allied to the development of the fins. The median fin that originally extended from the head of the animal to the tail has in the course of its development gradually retreated toward the posterior portion of the body until it is represented by a single caudal fin and one or more separated elements called from their positions the dorsal and the anal fins. The caudal fin has assumed different positions in relation to the terminal portion of the

spinal column. In the original condition the dorsal and the ventral parts of the fin were equally developed, and the vertebral axis divided the fin into two equal parts, so that the fin presented a rounded or slightly acuminate appearance. This is called the diphycercal condition. Another, and a very common condition among the more primitive forms of fish, is where the ventral portion of the caudal fin is developed at the expense of the dorsal, and the terminal portion of the vertebral axis is bent upward at the end. This is called the heterocercal condition. The form most commonly found in the modern forms of fishes is that in which both the dorsal and the ventral portions of the caudal fin are developed more than the main portion of the fin, but about equally themselves. This is called the homocercal condition, and was for a long time considered as the primitive condition, or at least more primitive than the heterocercal. It is shown to be untrue by the fact that even in the highest types of the bony fishes the extremity of the notochord is bent upward as in the heterocercal form of the tail. The progress of development of the tail seems to have been from the diphycercal through the heterocercal to the homocercal.[1]

The oldest remains of fishes that are definitely known come from the Upper Silurian and the succeeding rocks as high as the Carboniferous. The group called *Ostracodermi* has long been denied a position among the fishes by certain authors, the principal objection being the seeming lack of any lower jaw, which is regarded as one of the principal characters of the vertebrates. Because of this feature and the appearance of some of the forms which is similar in a general way to that of the Trilobites, the group has been considered as belonging to the *Crustacea*, but there are so many other characters that unite them with the

[1] A discussion of the facts here pointed out, with much more that is valuable to the student, will be found in a recent book by Bashford Dean, *Fishes, Living and Fossil*, an outline of their forms and probable relationships, Columbia University Biological Series, Macmillan & Co., 1895. This book takes up the various forms of fishes in a popular way that will not be beyond the student of geology who has the principles of biology. The large number of excellent illustrations will be found to be of great value in getting an idea of the fossil forms.

fishes that no less an authority than Smith-Woodward has placed them among the fishes. In general, the group is distinguished by the fact that the bones are not ossified; that the paired fins and the lower jaw are absent, and that the anterior part of the body is covered by large, bony plates that are developed in the skin and have no connection with the cartilaginous skeleton. The group is divided into three families: *Pteraspidæ*, *Cephalaspidæ*, and *Pterichthidæ*.

Pteraspidæ.—This family is confined almost exclusively to the Devonian, the Old Red Sandstone of England and Scotland. It contains the simplest and most archaic forms of the *Ostracodermi*. The anterior part of the body was covered by two large plates, a superior and an inferior, that served as a complete armor for that part of the body. The eyes protruded from openings formed by notches in the adjacent edges of the two plates. The upper plate is sometimes marked by grooves that are supposed to indicate the course and distribution of sensory tracts such as are found in the skulls of the shark and many of the more advanced types of fishes. The posterior part of the body was covered by many small rhomboid scales. It is probable that the forms were bottom feeders, and that the common food was the abundant molluscan fauna of the Devonian seas. *Pteraspis* and *Holaspis*, from the Devonian of England, and *Palæaspis*, from the Upper Silurian of Pennsylvania in the United States, are the best known of the family.

Cephalaspidæ.—In many respects the members of this family resemble the last, the anterior part of the body is covered by well developed plates, while the posterior portion is protected by rhomboid scales. The size was, in general, smaller than either of the other families, seldom reaching more than a foot in length. The head was large and curiously like that of a Trilobite in external appearance. The anterior edge was rounded, and there were two lateral posterior extensions in a position analagous to that of the genal spines in the Trilobites. The eyes were located near the center of this plate. The scales that formed the protection of the posterior part of the body are

large and arranged in rows, the mid-dorsal row developing an acuminate ridge that has the appearance of a dorsal fin. The tail was distinctly heterocercal. In some of the more perfectly preserved specimens there seems to be an indication of the presence of external gills at the base of the posterior lateral spines of the head plate. All the known forms are from the Upper Silurian and the Devonian rocks of England and Europe. Among the best known of the genera are, *Cephalaspis*, *Auchenaspis* and *Trematapis*

Pterichthidæ.—This family presents many important steps in advance of the other two, the anterior part of the body is not protected by single plates, but by an armor made up of the union of several small plates both upon the upper and the lower sides. The posterior portion was, as in the other forms, covered with small scales. Perhaps the most peculiar thing about the family is the presence upon the sides of the body, near the anterior end, of elongate, movable appendages that perhaps served as swimming organs, although in one of the later and more specialized of the forms the appendages become anchylosed to the adjoining plate, and lose all power of motion. These appendages are regarded as the homologues of the posterior extensions of the head plate of the *Cephalaspidæ*. The *Pterichthidæ* are most commonly known from the Devonian of the Old World. *Pterichthys*, *Asterolepis*, and *Bothriolepis* are well-known European forms. From the New World *Bothriolepis* has been described from the Devonian of Canada, and from the same horizon in Ohio incomplete remains have been described by Newberry as *Acanthaspis* and *Acantholepis*. It is necessary here to warn the student against a confusion that may arise between the old classification present in so many of the text-books and the one here used. The *Pteraspidæ*, *Cephalaspidæ*, and the *Placodermi* were regarded as orders of the highly artificial group, *Ganoidei*. The last order included not only the *Pterichthidæ*, but more highly developed forms that are now known to belong to the *Dipnöi*.

The *Elasmobranchii* are the most primitive forms that hold an

undisputed position among the fishes. Including both the sharks and rays, the group may be defined as made up of forms in which the skeleton is cartilaginous, the skin filled with fine calcareous particles (shagreen), the tail heterocercal, and the external openings of the gills mere slits in the skin of the neck unprotected by an operculum. In the previous sub-class there are no remains preserved of distinct vertebræ, but in the sharks the beginning of the vertebræ is seen in the formation of cartilaginous rings in the sheath of the notochord. These rings are of varying degrees of development in the different forms, in some forming mere circular bands around the chord, while in others they are nearly closed by the ingrowth of the cartilage that tends to segment the chord off into intervertebral elements. There is always attached to the superior and the inferior faces of the cartilaginous ring the neural and the hæmal arches that carry the spinal cord and the blood vessels.

The most primitive of the fossil sharks comes from the Lower Carboniferous of Ohio. This form, *Cladoselache*, is, in many respects, quite close to the hypothetical type form of all the fishes, the body is long and slender, and there were seven gill slits in the neck, which seems to be the number characteristic of the earliest forms. The unpaired fins have not progressed beyond the second stage of development, as outlined in the first part of this paper, that is, the fin fold is supported by small rods of cartilage, radials, that are not attached to the body wall. The paired fins are in a scarcely more developed condition, the lateral fold has disappeared, but the two lappets that represent the pectoral and the ventral fins have not progressed beyond the stage of the radial support, and are consequently of no value to the fish as swimming organs, but must have served merely as balancers. The tail was abruptly heterocercal. The whole form was rather small, not reaching a length of more than six feet at the outside.

Acanthodes, a rather small form from the Coal Measures of England, seems to present a step in advance of *Cladoselache*. The shagreen particles that are scattered throughout the skin

of most of the sharks are in this form enlarged into scalelike forms that fit tightly one against the other and afford a complete cover for the body. The paired fins are more strongly developed than in the previous form, and are better fitted for the purpose of balancing the body as well as assuming, to some slight extent, the function of locomotion.

Climatius, from Devonian Old Red Sandstone of Scotland, is of considerable interest from the fact that between the paired fins on the two sides there are developed many smaller fins, located along the line of the primitive fin fold. These are regarded as the remnants of the disappearing lateral body fold. The form represents a stage in this respect ancestral to both *Cladoselache* and *Acanthodes*, but is in other respects in advance of both of them.

Pleuracanthus, from the Permian, is one of the most interesting of the fossil sharks. It represents a stage considerably in advance of the forms already described. The radials of the median fins have separated off the proximal basal segments that afford the strong attachment of the fin to the body wall, and there is developed to some extent the dermal elements of the external edge of the fin that are found in the fins of the modern bony fishes. The paired fins present a very interesting condition, the fore limb having the character of a dipnoan fin, and the hind limb the characters of the more advanced type of the fish fin. To understand this condition it is necessary to go back to the formation of the paired fins from the lateral fin folds. The gradual development of the functional swimming fin was by the concresence of the basal and the radials to form strong, though somewhat flexible supports for the membrane of the fin. This was accomplished in two ways. In one the basals united and formed a long median axis upon each side of which the radials were attached after the manner in which the barbs of a feather are attached on each side of the quill. This type was originally supposed to be the most primitive form of the fin, and so it was given the name of *archipterygium*. In the other type the basals fused into one or more pieces that were

confined to one side of the fin, and the radials formed the other side ; this is the type of fin present in the more advanced fishes; it is called the *ichthyopterygium.* See Fig. 3.

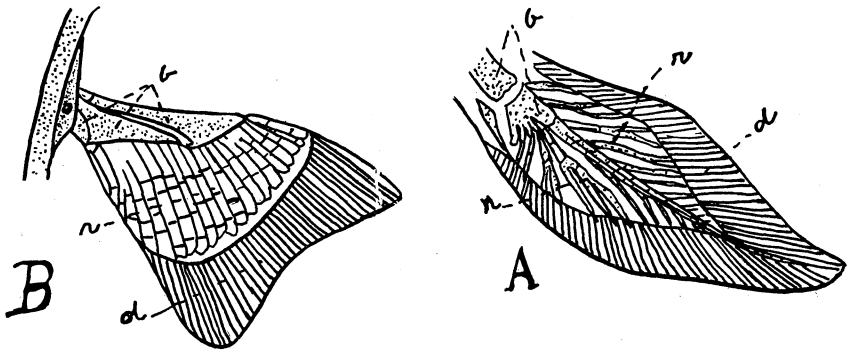

FIG. 3. *A*, archipterygium ; *B*, ichthyopterygium ; *b*, basals ; *r*, radials ; *d*, dermal margin.

Besides the peculiar condition of the fins, *Pleuracanthus* presents other remarkable features. Notable among these are the presence of a large spine that projected from the posterior edge of the skull, and the fusion of the shagreen denticles on the superior surface of the head into numerous dermal plates. In *Pleuracanthus*, as well as the forms previously mentioned, the center of the vertebræ had not yet become very well developed, and all that is found in the preserved specimens is the line of neural arches above the position of the notochord and the hæmal arches below.

Chondrenchelys from the Carboniferous of Europe was in many respects similar to *Pleuracanthus*, but there is one point of decided advance, the vertebræ were well formed, though still cartilaginous, and the inner part of the cartilaginous vertebral ring was well filled so that the chord was divided into segments by constrictions at the center of the vertebræ.

With the appearance of the sharks of the type of *Chondrenchelys*, the modern form is outlined, and since the Carboniferous there has been no great change in the general structure

of the group. One thing is important, however, and that is the changes that took place in the teeth of the many forms that were developed during the Carboniferous time. There seems to have been developed two types of teeth that indicate a very different mode of life. In one of these groups the teeth became flattened and adapted to crushing or grinding the shells of molluscs and crustaceans that formed the food supply. The surfaces of the teeth were sculptured in the most intricate manner, affording an enlarged and more efficient triturating surface. The different patterns of this sculpture seem almost endless. To these forms have been given the name of the "pavement-toothed sharks." *Janassa*, *Petalodus* and *Cochliodius*, all from the Carboniferous rocks are perhaps the best representatives of the group. *Cestracion*, the modern Port Jackson shark, is the single living representative. In the second group the teeth were developed in accordance with the demands of a more active and rapacious habit. They are more or less triangular in outline, and the edges are frequently finely serrated, affording a very firm hold as well as forming most efficient cutting organs. This type reached its development later than the pavement-toothed forms. The largest form, *Carcharias*, in which the teeth reached a length of six inches, is known from the Eocene of both the Old and the New Worlds. Other typical forms are *Sphenodus*, *Lamna*, and *Carcharodon* from the Mesozoic of Europe and many forms that are regarded as subgenera of *Carcharias* in North America.

One type of fossil that must be mentioned is the *Ichthyodorulite*. These are detached spines that are found in great abundance in the Carboniferous and Mesozoic rocks, and from which a large number of genera have been named. In the modern sharks the anterior end of the fins, and especially the dorsal fin, is frequently strengthened by the development of a strong spine that serves as a cutwater. These spines were much more strongly developed in the more primitive sharks, and were subject to the greatest degree of modification in form, structure, and ornamentation. As they were so strong they would naturally

be preserved through the accidents of fossilization more often than the softer structures of the skeleton.

The Rays or *Batoid* branch of the *Elasmobranchii* are of doubtful origin, other than the fact that they differ from the true sharks only in the modifications that are attendant on the extreme flattening of the body due to the habit of bottom feeding. They probably originated as far back as the Carboniferous time, although well-preserved forms are not known from rocks earlier than the Jurrassic. *Rhinobatis*, an existing genus, is known from the Oolite.

The part played by the sharks in the waters of the Palæozoic oceans seems to be very much the same as that played by the recent bony fishes in the modern waters. The variety of forms was seemingly endless, and the adaptations to various conditions of life, and to different means of obtaining food, bear witness, not only to the large number of forms, but to the strength and dominance of the type.

The *Holocephali*, the Chimeroids, is a peculiar, aberrant group, that is allied on the one hand to the sharks and on the other to the Dipnoans. The structure of the fins and the vertebral column is the same as in the sharks, but the structure of the head and the arrangement of the teeth is almost the same as the dipnoans. There is a single broad dental plate in the lower jaw, and two plates in the upper jaw instead of numerous isolated teeth. The surface of these tooth plates is variously modified by the addition of knobs, ridges, and other irregularities, to increase the grinding surface. Little is left of the fossil forms but the teeth and the spines that stood at the anterior end of the dorsal fin as in the sharks. Fossil forms are *Ischyodus*, *Myriacanthus*, and *Squaloraja*, all from the Mesozoic.

The *Dipnoi* are, perhaps, the most peculiar of all of the fishes. For a long time considered as the linking type between the fishes and the amphibians, they are now generally regarded as a degenerate group that originated from the stem of the Crossopterygian *Teleostomes*. They are characterized by the absence of a connecting bone, the quadrate, between the skull proper

and the lower jaw. This condition, called autostylic, is found in the preceding group. Other characters are the modification of the swim bladder, in the living forms at least, as a breathing organ that assumes to some extent the structure of the lungs of the land vertebrates, the presence of tooth plates instead of teeth in the jaws, the archipterygial structure of the fins and the diphycercal tail. At the present time there are only three genera of the group living, but their wide distribution points to a very great development in earlier times. The existing genera are *Protopterus* from Egypt, *Ceratodus* from Australia, and *Lepidosiren* from South America. In these forms, as in the fossils, the vertebræ are incompletely ossified, the centrum remaining cartilaginous, while the upper and the lower arches are fairly well ossified. The major portion of the skeleton is well ossified, thus showing a condition in advance of the sharks and Chimeroids.

The *Dipnoi* are an exceedingly ancient group; even as early as the Devonian they had developed most of the characters that distinguish them from the other fishes. While it is altogether probable that they originated from the primitive shark stem, the point of origin seems to be totally lost, for the well-developed Dipnoans are found contemporaneous with the earliest of the sharks. Of the early *Dipnoi*, perhaps the most interesting is *Dipterus* from the Old Red Sandstone. This form had well-developed cycloidal scales, the type of the modern fish scale, while the sharks still had the shagreen denticles, and the Ostracoderms the thick, bony, rhomboid scales so characteristic of the early fishes. It had the skull protected by a roofing of dermal plates, and the teeth modified into large plates, with rough triturating surfaces. The plates were arranged as in the *Holocephali*, two in the upper jaw and one in the lower jaw of each side.

Phaneropleuron, from the same horizons in Scotland, is more primitive in some of the characters; for instance, the jaws are provided with many small, conical teeth, and the dorsal fin is continuous instead of being broken up into two or three seg-

ments. Specimens of this genus are known from the Devonian rocks of the province of Quebec in Canada. *Ctenodus*, from the Carboniferous of England, *Holodus* and *Palædaphus* from Devonian of Europe, *Mylostoma* from the Devonian of New York, and *Gnathorhiza* and *Strigilina* from the Permian of Texas, are all characteristic forms that have been described from the teeth.

A division of the *Dipnoi*, the *Arthrodira* are of especial interest, as they were at one time regarded as belonging with the *Pteric thidæ* in an order the *Placodermi*. The discovery of well-developed lower jaws and paired fins demonstrated that they could not belong among the primitive *Ostracodermi*, and the discovery of the manner of the articulation of the lower jaw to the skull showed that they belonged among the *Dipnoi*. They are among the most ancient of the fishes, ranging from the Upper Silurian to the Carboniferous. In the United States a large majority of the known remains have been taken from the Waverly Shales of Ohio. In Europe they are found in the Devonian Old Red Sandstone of England and Scotland. They were powerful, armored, predatory forms, in many cases of large size, that must have been a match for the largest sharks of the time. The armor in some of the genera was between two and three inches in thickness. The armor seems to have been confined in most of the forms to the anterior portion of the body, which has led to the belief that perhaps they buried the posterior part of the body in the mud and lay in wait for their prey rather than seeking it out and depending on their rapidity of movement and powerful jaws to obtain the mastery.

Coccosteus, a rather small form from the Devonian of England, is one of the best known of the group. It did not reach a length of more than one or two feet. The anterior part of the body is covered with an armor made up of several plates that extend back to about the middle of the body. The centra of the vertebræ are not preserved but the upper and lower arches outline the notochordal column. The dorsal fin is in the stage of the basals and radials and the posterior pair of fins is united to a distinct pelvic girdle. The armor of the

anterior portion of the body was very hard and polished in appearance, looking like the enamel scales of the "Ganoid" fishes and covered with small tubercles that were divided by the course of rather deep sensory canals. The armor plates were purely dermal in character having nothing to do with the true skeleton which was still made up of cartilage. One very peculiar thing was the presence of a very strong joint between the plates covering the head and those covering the shoulders. This joint must have permitted a great degree of motion in the vertical direction between the head and the body, though the purpose of such a motion is not understood. The posterior part of the body was covered by a thick integument entirely devoid of scales such as are present in the *Ostracodermi*.

The American forms of the *Arthrodira* were in general much larger and better developed than the European ones. They reached a total length of as much as ten or twelve feet and the sculpture of the armor and the variety of forms presented in the development of the jaws bear witness to the great variety of genera developed. The arrangement of the teeth is somewhat as in the Dipnoans, that is there were no separate teeth bordering the jaws but there were dental plates that were attached to the edges of the jaw; one peculiar thing about the plates is that they were not fixed as in the Dipnoans but were to a greater or less extent movable. In general the body form was like that of *Coccosteus* but the modifications of the tooth plate presents a very remarkable series. In *Dinicthys* they are developed as sharp cutting edges with a strong notch near the anterior end, in *Titanicthys* as a simple cutting edge, in *Trachosteus* and *Diplognathus* the edges of the plates were serrated and presented the appearance of being set with isolated teeth as in the ordinary arrangement of the fish jaw.

The last of the subclasses of the fishes is the *Teleostomes*. This group includes the old orders *Ganoids* and *Teleosts* that have been used for so long and are still commonly met with in the text-books of geology. The main distinction between them as seen by the geologist is the presence in the Ganoids of bony,

rhombic scales and in the Teleosts of horny, cycloidal scales. It is readily shown that these characters are of the most superficial nature and the condition of one group is easily found in the other, still as a general thing it may be said that a majority of the older forms had the rhomboid type of scale and the modern forms have the horny type. Bashford Dean discusses the relationships and descent of the Teleostomes in the following words, p. 145: "Johannes Müller, when separating Ganoids from Teleosts, recognized clearly even at that early date (1844) that the majority of the structural differences of these forms were bridged over in exceptional instances; there were thus Teleosts with bony body plates, as well as, it was afterwards found, a Ganoid, (*Amia*) with herringlike cycloidal scales. But he believed that three structural characters of the Ganoids separated them constantly from all Teleosts, and warranted the integrity of the groups."

These distinguishing characters were:—

I. A contractile arterial cone, containing rows of valves.

II. An intestinal spiral valve.

III. The interfusion (chiasma) of the optic nerves.

It was not until these differences were shown to be of little morphological importance that the two groups were merged in that of the *Teleostomi* (Owen, 1866). Thus transitional characters of the arterial cone of *Butrinus* were discovered by Boas. The Teleost, *Cheirocentrus* was found to present Ganoidean intestinal characters, and the optic chiasma, as Wiedersheim demonstrated, could no longer be regarded as of taxonomic or morphological value.

The descent of the Teleostomes, like that of the other groups, has long been a matter of speculation. Their affinities with the Dipnoans are generally admitted (Gunther, Gegenbaur, Haeckel, Smith-Woodward). Rabl derives them directly from a Selachian stem, regarding the Dipnoans as later evolved Ganoidean forms. Beard, on the other hand, even goes so far as to entirely separate the Teleostome stem from that of the shark, lungfish, an amphibian, deriving it with a close kinship

to the *Petromyzonts* (*Marsupiobranchii*), from the earliest vertebrates. Palæontology, however, has lately been giving rich contributions to this disputed problem, and there can at present be little doubt that the conditions in fossil fishes have demonstrated that in most ancient times Dipnoan and Teleostome were closely approximated. Although even in the earliest fossils they may be distinguished (*e. g.*, by the arrangement of the head-roofing derm bones), yet, as Smith-Woodward has noted, forms occur too clearly transitional to indicate anything less than genetic kinship. The Crossopterygian, whose ancient structure is well known, may well have been derived from an ancestor common to the Ctenodont (Dipnoan) and the Holoptychian; so that the gradual nearing of the Teleostome stem to that more fixed, of the Dipnoan, is a strong suggestion of its derivation. The later descent of the Ganoids from an ancestor closely akin to, if not identical with the Crossopterygian, is usually conceded. Teleosts, first occurring in the Cretaceous, are by evidence of fossils the almost undoubted survivors of an extensive group of transitional Mesozoic Ganoids. But whether all Teleosts are to be deduced from a single ganoidean phylum can at present hardly be established. Thus catfishes, or Siluroids, appear in many structural regards closely akin to the sturgeon; but as their fossil remains are lacking before the Eocene — when however, they appear to have been in every way as highly evolved as in recent forms — little clew has been given to their descent.

Teleostomes may, in the present connection, be briefly characterized in their two principal subdivisions.

I. *Crossopterygian*, the more archaic group, uniting the characters of shark, lungfish, and ganoid, retaining the ancient cartilaginous fin bases, radials, and basals in their lobate fins; in some forms (*Holoptyhchius*), the concrescence of the basal parts of the unpaired fins passing through the same evolution as those of the paired fins. Represented in the surviving *Polypterus* ("*Bichir*" of the White Nile) and in the slender *Polypteroid Calamoicthys* (of Calabar), and in the extinct *Holoptychius*, *Undina*, *Diplurus* and *Coelancathus*.

II. *Actinopterygian*, the spine-finned Teleostomes. Fins supported by dermal rays; ancient fin support greatly reduced, implanted in the body wall. Includes *Chondrosteans* (Ganoids) and *Teleocephali* (Teleosts).

Among the fossil forms of the Crossopterygians *Gyroptychius* and *Osteolepis* from the Old Red Sandstone of Scotland are very similar to the early Dipnoans in the general appearance of the body. The tail is somewhat heterocercal and the dorsal fin is divided up into segments; but the teeth are numerous and arranged along the edges of the jaws instead of being reprerented by single plates. The entire body was covered by solid, bony scales the outside of which were covered by a layer of shining enamel. The anterior pair of the paired fins is approaching the condition in the Dipnoans, the archipterygium.

Holptychius, from the same locality and horizon as the last, is peculiar in that even at that early date it had developed the cycloidal, horny scales of the modern fishes, both the anterior and posterior paired fins are archipterygial in structure and the caudal fin has become nearly diphycercal by the fusion around the end of the body of the dorsal fins, the caudal and the anal. *Eusthenerpeton*, from the Devonian of Canada, is very similar to *Holoptychius*.

Diplurus, from Triassic of New Jersey, and *Undina*, from the Jurassic of England, present the last stage in the development Crossopterygians. They show an amount of specialization that indicates the extent to which the group had developed and the necessity for adaptation by its members to the most peculiar conditions to maintain an existence. *Undina* was short and very broad. The tail is especially broad and presented a very peculiar appearance, as the end of the spinal column extended beyond the broad psuedo-caudal fin formed by the posterior dorsal above and the anal below. The centra of the vertebræ are still unossified and the bases of the fins are reduced to single pieces of bone. In both this form and *Diplurus* the air bladder was ossified to a considerable extent so that it is preserved in the cavity of the body. *Diplurus* was greatly shortened in the body

by the enormous development of the psuedo-caudal fin, formed as in the case of *Undina* by the posterior dorsal above and the anal below, with the end of the vertebral column extending out beyond the two in a slender fin. The skull was relatively enormous and the jaws entirely edentulous.

Coelacanthus, from the Carboniferous of Ohio, is another of the highly-specialized Crossopterygians. The fins, scales, and general contour of the body is that of a modern bony fish, and it is only upon close examination that the fins were found to be of the archipterygial type and the caudal fin formed in the same way as the same fin in *Diplurus* and *Undina*.

The Actinopterygians are separated into two groups, the *Chondrosteans* and the *Teleocephali*. The first of these groups is very similar in many of its characters to the Crossopterygians, the most important difference and the one that marks the separation of the two greater groups is the structure of the fins. Instead of the lobate, or archipterygial type of fin with the well-developed basals and the symmetrically-arranged radials and fin rays, the basals have almost entirely disappeared and the fin has developed the monoserial structure, *i. e.*, the basal supports are confined to the most proximal part of the fin, and the rays are developed on one side only of the supports.[1] The skeleton is still cartilaginous and the scales are bony and covered with enamel.

Elonicthys, from the Permian of Europe, is a typical one of these forms, the body was somewhat elongate and the scales were narrow. *Eurynotus* from the Calciferous limestone of Scotland, *Cheirodus* from the Coal Measures of Scotland, and *Microdon* from the Jurassic of France, exhibit stages in the gradual development of a great vertical expansion of the body with an attendant shortening and flattening. In the last form there were developed flat crushing teeth instead of the sharp, conical form.

Aspidorhynchus, from the Jurassic of Solenhofen, was an elongate form much like the modern garpike in appearance

[1] See Fig. 3. Ichthyopterygium.

The body was protected by large enameled scales, and the head terminated in a long and sharp rostrum.

Palæoniscus is one the most important of the fossil *Chondrosteans*. It has a remarkable time range extending from the Palæozoic to the Mesozoic and developed a very large number of species. It is supposed to be the form that stands nearest to the ancestral type connecting the modern garpikes and the sturgeons.

These forms seem to have culminated in the modern sturgeons, in which the scales have almost entirely disappeared. In *Acipenser* a few rows of large dermal, enameled plates is all that is left, while in such forms as *Polyodon*, the spoon-billed catfish, the skin is entirely naked.

A second group of the *Chondrosteans*, developed mostly in the Mesozoic, had much more the appearance of the pure bony fish. The scales were small and rounded, and the fins are similar in shape and arrangement to some of the Teleocephali. The bones are calcified and the tail is nearly homocercal, but the vertebræ are still unossified and the notochord is prominent. The modern *Amia*, dogfish, is a surviving member of the group. Among the fossil forms are *Caturus*, *Megalurus*, and *Leptolepis*, from the Jurassic of Solenhofen. The first two of these are important in showing the formation of the vertebræ from the gradual development of bone in the centrum starting from the bases of the upper and the lower arches. In the first two of these forms the base of each arch is joined to a half-moon shaped element that is broad at the base and comes to a point at about the center of the centrum, the two together forming a ring that surrounds the notochord. In *Eurycormus*, from about the same horizon as the last, the same condition prevails in the vertebræ of the dorsal region, but in the tail the wedge-shaped half-moons are completed into bony rings and each vertebra is represented by two of these rings. (A condition that will be found of great interest in the consideration of the morphology of the vertebræ of certain of the amphibia.) The beginning of the process of forming the bony vertebræ by the growth of the

peripheral portion of the ring is seen in the more primitive forms, *Microdon* and *Pycnodus*. In the first of these the bases of the arches are expanded and terminate in rounded and flattened processes that cover the sides of the notochord to a considerable extent, but do not meet in the middle line. In the second form the bases of the arches are more expanded than in the first and the edges of the expanded portions are serrated so that they interlock both with the ones immediately before and behind them and with the one on the opposite side of the notochord.

There have been mentioned here, of course, only the forms that show to some extent the modifications and the lines of development along which the Ganoids traveled. The waters of the Mesozoic lakes and oceans were swarming with members of the group that presented almost as many varieties of structure and form as do the modern bony forms. Because of the strong, interlocking, enameled scales the whole body of the fish is commonly preserved, but the internal skeleton is much less commonly available, so that the most of the forms are known from characters of the scales and the position of the fins, both of which characters are, to a certain extent, unsatisfactory and unreliable.

The *Teleocephali*, the group generally known as the Teleosts, seem to have appeared at about the beginning of the Mesozoic time though it did not reach a great degree of development until near the close of that period and during the Tertiary time. The members of this group differ from the other forms of fishes in the complete calcification of the bones of the body and the nearly complete loss of the notochord by the development of the solid vertebræ which divides it up into intervertebral segments. The scales are horny and rounded, loosely attached to the skin and overlapping in the style of shingles. The fins are formed almost entirely by the dermal fin rays, the basals, and the radials being greatly reduced. Dean says, p. 167: "Fins are dermal structures, their ancient basal supports hardly to be distinguished; the primitive tail structure is so masked by

clustered and fused elements that its heterocercy is scarcely apparent. In short, the most widely modified conditions can be shown to exist in Teleosts in almost every structural character, as in gills, teeth, opercula, circulatory and urogenital organs, sensory structures and nervous system. They have evidently been competing keenly in the struggle for survival, for in every detail of form or structure the most varied conditions exist. In addition to these structural adaptations of the Teleosts, changes in coloration have been rendered possible by the transparency of their scales; and in their different families these changes have taken place often with striking results." It is impossible to go into the forms of the *Teleocephali*, for they are so many and varied that there is no outline even, that the limits of the purpose of this paper would permit. A study of the fossil Teleosts would be practically a study of the osteology of the recent forms.

REFERENCES:

DEAN, BASHFORD, Fishes Living and Fossil. Macmillan & Co., 1895. Besides the subject-matter this book contains an excellent bibliography of the most valuable works on fishes.

ZITTEL, KARL von, Handbuch der Paleontologie, Paleozoologie. III Bd.

NEWBERRY, J. S., Paleozoic Fishes of North America. Monograph XVI of the U. S. Geol. Survey, 4to, 340 pp., 53 pls.

WOODWARD, A. SMITH, Catalogue of Fossil Fishes of the British Museum. Vols. I, II, III, 1889–1895, London.

GILL, THEO., Fishes: Standard Natural History. Boston, 1895.

E. C. CASE.